

BREEDING BIOLOGY AND SYSTEMATIC RELATIONSHIPS OF THE STILT SANDPIPER

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THE subfamily Calidridinae (family Scolopacidae) includes 24 species of small to medium-sized sandpipers, nearly all of which are entirely restricted as breeding birds to arctic or subarctic areas. Eighteen species are included in the genus *Calidris*, the remaining six each being assigned to a monotypic genus (Jehl, 1968c). Many species of *Calidris* are quite similar morphologically, perhaps reflecting a fairly recent radiation in tundra areas. Within the entire subfamily, however, there is wide diversity in bill morphology, sexual size dimorphism, and breeding biology. To date, studies of morphology and plumage characters have not resulted in any real understanding of calidridine evolution, and other approaches are necessary. Studies of the evolution of social systems by Pitelka, Holmes, and others seem to offer a significant approach to the problem, but their value is dependent upon detailed data on the biology of individual species.

In recent years there has been renewed interest in the biology of calidridine sandpipers, in part because of their important position in arctic ecosystems, and fairly complete accounts are now available for a few species (e.g., *Calidris melanotos*, Pitelka, 1959; *C. fuscicollis*, Parmelee et al., 1968; *C. alba*, Parmelee, 1970). The outstanding studies on Dunlin (*C. alpina*) by Holmes (1966a, b, c, 1970, 1971a) in Alaska and by Soikkeli (1967, 1970a, b) in Finland are the most complete treatments of the ecology and breeding adaptations in any sandpiper.

This paper deals with the Stilt Sandpiper (*Micropalama himantopus*), a little-studied species which has generally been considered a somewhat aberrant member of the calidridine complex. Most of the literature on the breeding biology of this species is anecdotal, incomplete, or even erroneous (e.g. Farley, 1936), but important contributions have been made by Sutton (1961), Parmelee et al. (1967) and Jehl (1970).

METHODS

Field work was conducted near Churchill, Manitoba, mainly in the summers of 1965, 1966, and 1967; a few additional observations were made in 1964. I was present in the Churchill region between 28 May–2 August 1964, 29 May–22 July 1965, 2 June–26 July 1966, and 9 June–13 July 1967. In 1964 and 1965 I arrived before the earliest migrants and departed after the adults had migrated southward.

The bulk of my observations were conducted within two miles of Fort



FIG. 1. The approximate breeding range of the Stilt Sandpiper (cross hatched). Solid circles within the cross hatched region indicate areas from which breeding specimens were examined. The three circles in western Alaska indicate areas from which presumed breeding specimens were examined. The star indicates a breeding locality mentioned in the literature.

Churchill. Other observations, particularly searches for banded birds, were made in suitable habitat throughout the region and up to eight miles east of Fort Churchill.

Birds were trapped at the nest using a simple hardware cloth trap. Most birds accepted the trap within 30 minutes, and efforts to trap warier birds were discontinued after a few attempts. Trapping had no adverse effect on reproductive success, except that several eggs were cracked as adults sought to escape. The birds were then banded, measured (see Jehl, 1970), and dyed on the rump with a Magic Marker for individual identification. The color markings were retained for about three weeks before fading into obscurity. Central rectrices were removed from most birds for molt studies. In 1964 and 1965 a few birds were mist-netted at feeding ponds, but this procedure proved to be extremely inefficient.

There is little sexual plumage dimorphism in this species. On the average,

the ventral barring of males is blacker and lacks the brownish cast of that found in females, but there is so much overlap that sexing by this character alone is unreliable. As in many other calidridine sandpipers, females average larger than males (Jehl, 1970: Table 1). I determined sex from behavioral characters associated with courtship or territorial defense, and from the knowledge that males almost invariably incubate by day, females by night (see below). Measurements were used to confirm the sexing of some birds, and several birds were shot for positive identification. All statements regarding the roles of the sexes in this paper are based on birds of known identity.

Banding studies showed that birds tended to mate with their mates of the previous year, and that the breeding behavior of experienced pairs differed from that of inexperienced pairs. To differentiate, I refer to *old pairs*, i.e., pairs known from banding to have been formed in a previous season, and *new pairs*, i.e., pairs not known to have formed before (see also Jehl, 1970: 312).

Specimens were collected throughout this study for data on molt and breeding condition. In addition, for studies of geographic variation, I examined 427 specimens borrowed from the American Museum of Natural History, United States National Museum, Carnegie Museum, Museum of Comparative Zoology, Chicago Natural History Museum, Cornell University, Museum of Vertebrate Zoology, Royal Ontario Museum of Zoology, National Museum of Canada, the University of Michigan Museum of Zoology, and from George M. Sutton and David F. Parmelee.

DISTRIBUTION

As a breeding bird the Stilt Sandpiper is restricted to the North American tundra, where it occurs chiefly in the Subarctic and Low Arctic zones (Johansen, 1963). The nesting range extends westward from Cape Henrietta Maria, Ontario, to Alaska, though the precise western limits are unknown (Fig. 1). Bailey (1948) knew of only one Alaskan nesting record. However, Brooks (1915) suspected nesting near Demarcation Point, and I have examined 10 other Alaskan specimens collected on dates when one would expect nesting activity; one of these was collected only 65 miles south of Barrow. The occurrence of spring migrants at Anaktuvuk Pass (Irving, 1960), in north-central Alaska, seems too regular to be fortuitous, and it may be that the species is expanding westward.

According to the A.O.U. Check-list (1957), the Stilt Sandpiper winters "in South America (range imperfectly known) from Bolivia, central western Brasil (Mato Grosso), and Paraguay south to Uruguay, and central eastern Argentina (Province of Buenos Aires)." However, its winter range is cer-



FIG. 2. Typical breeding habitat of Stilt Sandpipers at Churchill, Manitoba, consisting of well-drained sedge marshes with scattered tundra ponds.

tainly more extensive and probably far more northerly. In recent years small numbers have wintered as far north as the Salton Sea, California (McCaskie, 1970) and concentrations have been found near San Blas, Mexico (Alden, 1969) and in northern Venezuela (McNeil, 1970). There are also a few recent records for southern Peru (Hughes, 1970) and northernmost Chile (A. W. Johnson, pers. comm.). Previously published records for southern Chile by Peña and Barros (Johnson, 1965) are based on misidentified Wilson's Phalaropes (*Phalaropus tricolor*; Jehl, unpubl.).

HABITAT

At Victoria Island, Stilt Sandpipers occupy a variety of habitats, from "wet tundra areas upgrown to fairly high willows" to "higher, much drier slopes with moderate vegetative cover, avoiding the truly barren ridge tops" (Parmelee et al., 1967). At Churchill their habitat preference is much less broad. There they occur mainly in well-drained sedge (*Scirpus caespitosus*) meadows that are interrupted by old beach ridges, eskers, or other elevated areas which provide dry nesting sites early in the spring (Fig. 2). Some nesting areas also contain small ponds varying in depth from a few inches to several feet. In late spring the tundra may be flooded when the earliest

migrants appear, with patches of snow remaining in sheltered areas. Run-off is extremely rapid, however, and by mid-July the shallow ponds are dry.

Dominant plants on elevated areas are dwarf birch (*Betula glandulosa*) and heaths (*Rhododendron lapponicum*, *Andromeda glaucophylla*, *Arctostaphylos* sp., *Vaccinium uliginosum*, *V. vitis-idaea*). Other conspicuous plants include *Dryas integrifolia*, *Empetrum nigrum*, *Salix reticulata*, and *Cladonia* spp. Passerines occurring in this habitat are Savannah Sparrow (*Passerculus sandwichensis*), Smith's Longspur (*Calcarius pictus*) and Lapland Longspur (*C. lapponicus*). Common nesting shorebirds are Hudsonian Godwit (*Limosa haemastica*), Hudsonian Curlew (*Numenius phaeopus*), Dunlin, Least Sandpiper (*C. minutilla*), and Golden Plover (*Pluvialis dominica*).

ARRIVAL

Stilt Sandpipers begin arriving at Churchill in late May (earliest, 21 May: Mowat and Lawrie, 1955). The earliest migrants occur singly and within a day or so flocks of up to ten birds appear, flying low and fast northward over the tundra. The peak of migration occurs in the first days of June and by 6 June, even in late seasons, the bulk of local breeders have arrived. Migrants, which continue to pass through the region until mid-June, concentrate in marshes along the Churchill River or on the shore of Hudson Bay and avoid tundra areas.

Observations backed by selected collecting indicate that males tend to arrive a day or two in advance of females. This conclusion is supported by the high percentage of males collected throughout the breeding range in early June, and by the high but progressively declining proportion of males collected from migrating flocks in the northern prairie states and provinces from May through the first week of June (Jehl, unpubl.).

Soikkeli (1967) found that experienced Dunlin arrived somewhat earlier than birds nesting for the first time. Limited data indicate the same is true of Stilt Sandpipers, as territories of experienced birds are the first to be occupied. Experienced birds immediately return to their territories of the previous year. In late springs the sexes may appear on the territories almost synchronously and without studies of marked individuals one could justifiably conclude that pairing had been accomplished during migration. Knowledge of the entire breeding cycle of the Stilt Sandpiper renders this hypothesis untenable, and in fact, virtually impossible (Jehl, 1968a:519).

The suggestion of enroute pairing has been advanced for other arctic sandpipers (e.g., *C. alpina*: Holmes, 1966a) and seems logical in view of the severe constraints on the reproductive cycle imposed by the short arctic summer. However, Soikkeli (1967) found no evidence for pairing during

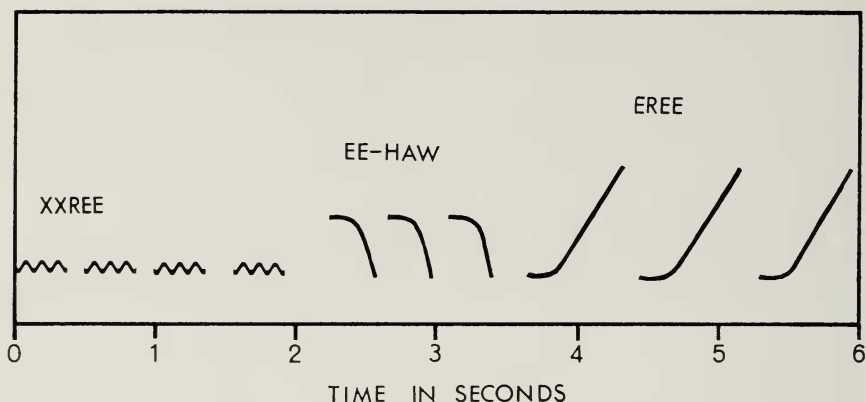


FIG. 3. Schematic representation of the flight song of the Stilt Sandpiper.

migration in Dunlin and argued strongly against that possibility. Recent studies have demonstrated strong site and mate fidelity in several species (*C. alpina*, Soikkeli, 1967; *C. mauri*, Holmes, 1971b; *C. minutilla*, Jehl, unpubl.). As knowledge of marked populations increases it becomes evident that most if not all cases of enroute pairing in sandpipers reflect only the strong homing ability and site fidelity of experienced breeders.

VOCALIZATIONS

Stilt Sandpiper vocalizations are no less complex, variable, and difficult to transcribe than those of other calidridine sandpipers. The most frequent calls and the contexts in which they are given are summarized below.

Eree.—A drawn-out ascending call given by flying males marking a territory. The call is delivered at a rate of one per second and may be given incessantly, save for pauses for breath, for periods of up to eight minutes. This is the “whine note” of Holmes and Pitelka (1964). It is also given by females.

Song.—The song is usually given in flight after a series of *eree* notes. It may be roughly transcribed as *xxree-xxree-xxree-xxree-ee-haw, ee-haw, ee-haw* (Fig. 3). After completing this portion of the song, the bird may revert to a series of *eree* calls, or, if about to land, will add on one or two *eree* notes before descending. The *xxree* note (I have sometimes transcribed it as *creek* or *craw*) is harsh and guttural, and as many as 14 may be run together. The *ee-haw* note has been likened to the braying of a donkey. When given from the ground the song is used in an aggressive context and is often accompanied by a typical calidridine Wing-up threat display. Females also sing, though less melodiously than males.

Errit (or *currick*, or *quo-ick*).—An insistent, slightly ascending guttural note that is used in several contexts. It is given by males that have landed after completing a territorial flight and apparently announces that the territory is occupied. A similar note was heard from a male that was attempting to attract a female to a nest scrape. The note may also indicate annoyance and is occasionally given by birds that have been flushed from the nest and are hesitant to return. Several *errit* notes may be run together as a threat; such a series introduces the threat song on the Peterson Field Guide record (Allen and Kellogg, 1962). A similar run-on call, slightly descending in pitch and reminiscent of a mechanical toy running down, was often heard from birds announcing their presence from a small hillock. This note is very similar to the alarm call of the Dunlin.

Trrrrr.—A rapid, gurgling, descending trill. I heard it on only a few occasions, for example, from a male threatening other Stilt Sandpipers at a feeding pond and from a male defending chicks, where it was accompanied by a Wing-up display. It appears to function as a low intensity threat and is similar to the trilling threat call of the Dunlin.

Oo-it.—A sharp alarm call given by birds with chicks. This note is rarely heard before late June and is an almost certain sign that the eggs have pipped or hatched.

Toi.—Apparently a contact note between members of a pair; rarely heard except in the interval after the pair has occupied the territory and before the start of incubation.

Kyow (sometimes *kyow-it*).—A strong threat note given, for example, to intruders at the nest or when chicks are disturbed (when it is alternated with *oo-it* calls).

Weet.—A soft contact note given by birds incubating pipped eggs or brooding small chicks.

TERRITORIALITY, COURTSHIP, PAIR FORMATION

Males begin to establish territories through aerial displays immediately upon arrival. The territorial flights follow no apparent pattern. A male may hover over an area for several seconds, make a wide circle over favorable nesting areas, or fly completely out of sight. Typically flights are prolonged, lasting as much as eight minutes. The male flies slowly at elevations of 20 to 60 m—his wings describing a narrow arc of only a few degrees above and below the horizontal, legs outstretched, and tail spread—giving the *eree* call almost incessantly. Occasionally, he glides with wings set at an angle of 30° above the horizontal and sings; this is a low intensity display, usually given when no other birds are in the vicinity. He may then fly off erratically, only to resume the display a few hundred meters away. Prior to landing, the male

sings once more, then raises his wings almost vertically and plummets earthward. Landing on a conspicuous spot, he holds both wings vertically for a moment before folding them. He surveys the territory, occasionally calling *errit*, which announces that the territory is occupied. Other birds passing over the territory are chased vigorously, but because of the distances over which the displays are performed, the rapidity of the chases, and the slight sexual plumage dimorphism, it is not always possible to distinguish chases from courtship displays.

Aerial displays largely suffice to establish and maintain territories and it seems that mainly air space is defended. Early in the period, intruders landing on the territory may be chased off. It is not unusual, however, for three or four males to land together on one's territory after a prolonged chase but without exhibiting any aggressive behavior.

Air space is strongly defended through the egg-laying period, but soon thereafter the duration and intensity of displays declines. By about a week after the clutch is completed males no longer give the Wing-up display on landing and they ignore other Stilt Sandpipers performing territorial flights over their area. Other species are generally ignored. Yet, in one area where Dunlin and Stilt Sandpipers nested in proximity aerial interactions were common. These included bouts of flight singing and occasional chases that continued through the first week of the nesting season. Although the flight songs and postures of these similarly-sized species differ, their general patterns of territorial display are similar (see Holmes, 1966a:9-10), and the interactions appear to constitute interspecific territoriality (cf. Murray, 1971).

Territory size can be determined only indirectly because of the virtual absence of ground displays and because aerial displays extend over such vast areas. In most suitable areas nests were 300-400 m apart and territory size approximated 15 to 20 acres. However, in a 50-acre study plot where five pairs nested in two successive years, only 60 percent of the area was suitable and nests of three pairs were aligned approximately 100 yards apart in one corner of the plot; territory size there approximated 3 to 5 acres. Even closer-spacing was achieved by two late-nesting pairs which squeezed into prime areas 48 and 53 m from other nests by delaying nesting for 7 to 10 days, until territorial behavior in the original occupants had waned.

The function of territoriality and nesting dispersal is often difficult to ascertain, both "protection from predators and feeding habits" being important (Lack, 1968:140). For territorial shorebirds, however, Lack (1969:143) concluded that territoriality is not related to food supply inasmuch as "the territories claimed do not usually include any of the feeding grounds, and the young are often taken from the breeding territory soon after they hatch." This conclusion applies to the Stilt Sandpiper, for neither adults nor

young obtain any appreciable fraction of their food from the nesting territory. In this species, territoriality spaces the population by setting a limit on the number of pairs that can begin nesting synchronously; as a result nests are less accessible to predators. However, the general applicability of Lack's conclusion requires further verification, as shown by Holmes' (1970) study of territory size in Dunlin.

Courtship.—Courtship begins as soon as females appear in the nesting areas and involves prolonged and spectacular aerial displays which extend over an extremely wide area. Males fly after females singing song after song. They attempt to fly slightly ahead of the female, then raise their wings almost vertically and sing frantically as they fall, tilting from side to side. After dropping earthward for 40 m or more, they resume the chase and repeat the entire performance. Often these displays involve several courting males, which are joined by territorial males defending their air space. Females apparently do not sing during these displays, but I have heard them utter a nasal *yaw, yaw*, as well as a churring note.

Mate and territorial fidelity.—Mate and territorial fidelity are high. Of 29 pairs studied between 1964 and 1966, 25 were known to be alive at the end of the breeding season, and 11 reunited the following year, annual re-mating rates varying from 42 to 50 percent. Of the 11 pairs, seven which had hatched young returned to their previous nest scrape; the remaining four pairs moved their nests 12, 18, 21, and 76 m. Two of the four pairs had failed to nest successfully, and one other pair had nested in an unusual location.

Not one member of the 14 pairs that did not reunite was found mated in that year, although a few were found defending territories; one male that occupied the same territory for three years was found defending a new area 900 m distant in the fourth year, when his mate did not return. Some unmated birds returned to their original territory after missing one breeding season. For example, two birds (one male, one female) banded in 1965 failed to nest in 1966 but in 1967 nested with new partners 150 and 300 m from their previous nests. Another male, whose nest was not located was found defending chicks $\frac{1}{4}$ mile from this 1965 nest.

Coulson (1966) found that if Black-legged Kittiwakes (*Rissa tridactyla*) failed to nest successfully the pair was not re-formed in the next year. In Stilt Sandpipers failure to reunite probably results from the death of the mate in most cases; 12 of 14 pairs which did not reunite had raised young, whereas two of 11 that reunited had not. It may also be caused by the delayed arrival of one partner (Soikkeli, 1967), but this did not seem to occur in the present study.

Pair formation.—The basis for mate selection in birds has not received

adequate experimental study. Verner and Engelsens (1970) hypothesized that the size or quality of the male's territory might be important in attracting females in Long-billed Marsh Wrens (*Telmatodytes palustris*), but their results were inconclusive.

In Stilt Sandpipers initial pairing is on the basis of size (Jehl, 1970), small males and/or large females being among the first to pair and hatch young. Presumably the birds evaluate each others' size through ground displays, since that could not be done precisely during the complicated aerial courtship. Ground displays associated with pair formation are described in other calidridines (e.g., *C. ferruginea*, Holmes and Pitelka, 1964) but I did not observe any in this species.

In old pairs, pair formation and mate retention seem to be largely a consequence of territorial fidelity. Females return to the territory, where they encounter their mate of the previous season and begin nesting at once. Although I was unable to obtain quantitative data, it was obvious that territorial and courtship behavior was reduced in their territories. In fact, the presence of one old pair was not even suspected until an egg appeared in the old nest. Nethersole-Thompson (1951:103) found that in the Greenshank (*Tringa nebularia*) new pairs were "always noisier . . . than are birds that have maintained or re-formed old associations." Morris and Erickson (1971) showed that pre-mating courtship behavior in Ring Doves (*Streptopelia risoria*) was not necessary for the reinstatement of a pair bond, even after members of the pair had been separated for seven months.

The pre-nesting behavior of old pairs constitutes a series of adaptations that permit rapid nesting. Pre-laying formalities are accomplished largely at the time of first pairing. Territorial fidelity insures that experienced birds need lose no time in seeking a nesting area, and by foregoing prolonged courtship displays or even choice of a nest site, old pairs can begin nesting as soon as environmental conditions permit. Early nesting is advantageous because the tundra dries rapidly, and chicks of late-nesting pairs may find it difficult to obtain food. The persistence of this mating system despite its major disadvantage—celibacy for a year if the mate fails to return—is evidence of strong selection for early nesting imposed by the short arctic summer.

NESTING

Stilt Sandpipers nest in relatively open areas of dry tundra, usually atop small sedge hummocks or on low, well-drained gravel ridges that cross the sedge meadows. The location of the nest bears no necessary relation either to the location of standing water (contra. Farley, 1936:16) or to nests of other shorebirds. I have found nests within 10 m of Hudsonian Curlew, 5 m

of Least Sandpiper, 4 m of Hudsonian Godwit and 25 m of Dunlin nests. Of more than 40 nests examined, only three were in atypical situations; one was atop a bulldozed pile of peat next to a road, and two were in very wet marshes. These were among the latest nests to produce young and were presumably made by inexperienced birds unable to secure territories elsewhere.

The nest, a scrape 95–120 mm wide and 25–35 mm deep, is made by the bird rotating its breast against the soft terrain; no lining is added. Often the scrapes are enlargements of pre-existing depressions, and one covered the entrance to a clogged lemming burrow. Most nests are fully exposed, although perhaps 15 percent were adjacent to a dwarf rhododendron or birch.

The male takes the lead in scrape-making whereas the female determines which scrape will be used for the nest. In one territory I watched the male make a scrape atop a sedge hummock. The female approached, giving a low chattering call, crouched briefly in the scrape, then walked away. Rejected, the male raised one wing and sang. He then flew to another hummock and began to toss plant material over his shoulder, calling *errit, errit*; the female gave no response. He continued to another hummock, where he continued calling and tossing debris, again without response. Both birds then resumed feeding. A nest was made in this area, but the original scrape was not used.

It is not uncommon to find five or more fresh scrapes in territories of new pairs. Old pairs tend to re-use their nest of the previous year, and many make no new scrapes. The old nest may or may not be cleared of debris, but even uncleaned nests are probably visited prior to their re-use, because my dog scented an old scrape in 1966 that contained an egg the next day.

Copulation.—In four summers I observed only one attempt at copulation. It occurred on the shore of a small pond at least 400 m from any nest site. A pair landed together, whereupon the female immediately crouched and gave a low gurgling call lasting 15 seconds. The male then attempted to mount, but lost his balance; the pair immediately flew off together.

Laying; eggs.—The normal clutch is four. At five nests found before the clutch was completed, the interval between successive eggs averaged 36 hours, with extremes of 26 and approximately 48 hours.

Eggs range in ground color from light green to olive green and are heavily dotted with dark brown. They are similar to Dunlin eggs but the ground color averages darker and dark markings are more extensive. Measurements of 121 eggs are: length, 34.6–39.9 (36.5) mm, $sd \pm 0.82$, C.V. 2.26; width, 24.5–26.8 (25.5), $sd \pm 0.33$, C.V. 1.37. I found no differences in egg size of four females whose clutches were measured in two consecutive years.

Role of sexes in incubation.—Continuous incubation begins after the final

egg is laid. At several nests females brooded at night, and perhaps sporadically during the day, after the third and occasionally second egg was laid. Once the clutch is completed, both sexes share incubation duties. As Parmelee et al. (1968:17) indicate, the role of the sexes in incubation is almost inflexible; the male incubates without relief during the "day" and the female at "night." At most nests I studied change-over occurred about 05:00 and 19:00; 95 of 110 observations (87 percent) of incubating males were made between 05:00 and 19:00; 44 of 57 observations (77 percent) of females between 19:00 and 05:00. Most of the exceptions reflect minor differences in change-over times at specific nests; at one nest, for example, the female did not relieve the male until 21:00. However, six females were trapped at midday early in incubation. In at least three of these cases the male had been incubating, but would not enter the trap, and the female came to the nest in response to his alarm calls.

Change-over behavior is simple. Usually the returning bird lands 10–25 feet from the nest without giving any prior announcement. The incubating bird may fly to the intruder, give a Wing-up display and sing, challenging the returning bird to "prove" its identity. More frequently, the incubating bird flies off immediately to a feeding area far removed from the territory.

In the Dunlin (Holmes, 1966a:11; Soikkeli, 1967:166) and in certain other calidridines, the male's share of incubation reportedly increases as hatching approaches, particularly in late-nesting pairs. I found no such pattern in Stilt Sandpipers, not even after the eggs had pipped.

A fairly rigid "male by day, female by night" incubation pattern characterizes several other shorebirds nesting at Churchill (58°50'N), including Least Sandpiper and Dunlin (Jehl, unpubl.). A similar pattern is found in Dunlin in Finland (61°30'N; Soikkeli, 1967) though at Point Barrow, Alaska (71°20'N) only the general pattern persists (Holmes, pers. comm.). As the Alaskan population enjoys continuous daylight during the nesting season, whereas Finnish and Churchill populations do not, one might speculate that timing breaks down in the absence of a dark period. This is unlikely, however, since Stilt Sandpipers on Jenny Lind Island (68°N), also on a continuous light regime, maintain the same pattern as Churchill birds (Parmelee et al., 1968).

Gonad development, renesting.—Males are capable of breeding as soon as they arrive. Although their testes have not attained maximum size, free spermatozoa are present in the lumina of some tubules (stage 5b of Selander and Hauser, 1965). Testicular volume increases to an average of 110 mm³ (maximum 226 mm³) by early June, decreases sharply in mid-June, and drops to 3 to 4 mm³ by the time males depart (Fig. 4). Ovarian development is not completed on arrival. The largest ova of newly-arrived females approxi-

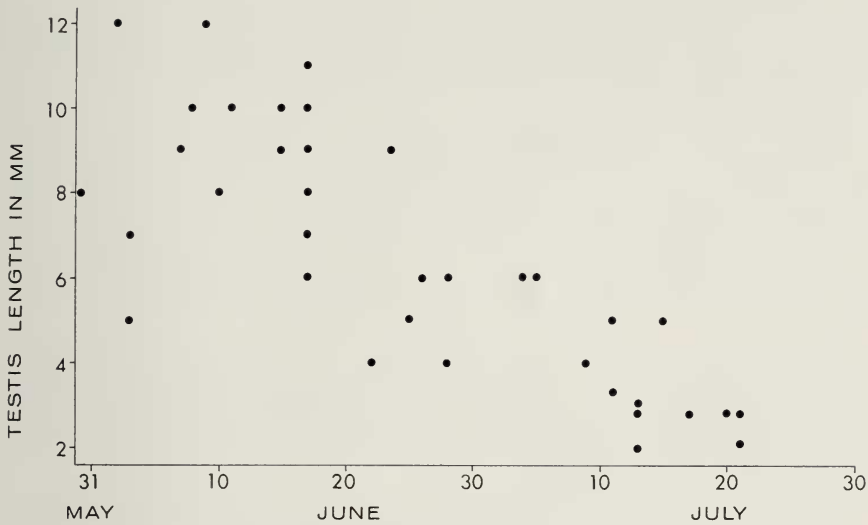


FIG. 4. Seasonal variation in testes size in Stilt Sandpipers.

mate 4 to 5 mm in diameter, enlarging to 9 mm within three to five days. A week after laying they average 4 mm and by the time of hatching 1 mm.

Because of the rapid gonadal regression, Stilt Sandpipers are probably incapable of producing a replacement clutch if their eggs are lost more than a week or so after laying. In this study I found no direct evidence for re-nesting, the only hint of that event being the late nesting of one old pair in 1966 nearly two weeks after other experienced breeders had nested. In 1938, after a severe snowstorm, Farley (1939) reported that many sandpipers re-nested, but the chronology of events suggests that the small clutches he reported were the remainder of the first clutches, the first eggs having been deserted.

Behavior during incubation.—The pair remains on or near the territory until several days after the clutch is completed, leaving only occasionally to feed. Early in the incubation period the male continues to defend air space over the territory, but through most of the period the birds remain so quiet that their presence may be unsuspected.

They generally ignore other birds on the territory, although I have seen males walk off the nest to threaten godwits and curlews that were returning to their nests only a few feet away. On several occasions I placed mounted Stilt Sandpipers and Short-billed Dowitchers in conspicuous locations on the territory and as close as one foot from the nest. The birds paid little attention, except to stare at the mounts for a moment before resuming incubating. Avian

predators, such as jaegers, hawks, and ravens, also evoke scant reaction, but their movements are watched carefully. Nevertheless, Stilt Sandpipers quickly leave the nest to investigate alarm cries of curlews and godwits directed at these same predators.

Rarely can a Stilt Sandpiper be surprised at the nest. When a human approaches within 75 to 100 m the incubating bird flies off inconspicuously only a foot or so above the vegetation for 50 m or more before climbing rapidly to a height of 30 to 50 m. Often the first clue to the presence of a nest is a bird flight singing overhead. The bird may then fly away for up to 15 minutes, before alighting 60 m away and cautiously sneaking back to the nest.

Birds flushed at the nest flutter off a few feet, then challenge the intruder with a Wing-up display or threat song; common displacement activities include vigorous preening of the neck and scapulars and tossing bits of debris over the shoulder.

Distraction displays are far less common than in those species (e.g., *C. minutilla*) which sit tightly and flush almost from underfoot. However, the display is similar to that of other calidridines in that the head is lowered, the wings are held slightly away from the body but are not spread, the back is hunched with back feathers ruffled, and the tail is drooped and fanned prominently. Williamson (1950:29) stated that this behavior, the "rodent-run display," "clearly owes its biological success to its semblance of a small mammal running away." In support of this hypothesis (p. 31), he likened the dark central upper tail feathers of some calidridine sandpipers, which may be obvious in the display, to the "lemming's dark-colored dorsal stripe." This interpretation has been widely followed (e.g., Armstrong, 1964) and the term "rodent-run" is now deeply ingrained in the literature (e.g., Brown, 1962). Nevertheless, I believe that the interpretation is anything but clear and that the name of the display is misleading and inappropriate. I find it inconceivable that any predator could mistake this behavior as that of a mammal. The calidridine species I have studied do not shuffle off furtively but make themselves conspicuous, occasionally giving plaintive calls. Duffy and Creasey (1950:28) noted that *C. maritima* "spared no pains to make its presence known." Further, the display is well developed in such species as *Micropalama himantopus*, *Calidris fuscicollis* (Drury, 1961) and *Calidris canutus* (Hobson, 1972), which lack dark central rectrices or upper-tail coverts. The simplest interpretation is that the birds are imitating weak and flightless sandpipers—and they do this very well.

Birds startled at the nest at the end of the incubation period also perform an "injury-flight" distraction display (Brown, 1962) but such behavior is rare. In this display they flop away conspicuously, beating their wings along

the ground and calling occasionally. One bird, alternating weak flights and short runs, led me more than 150 feet before it flew away.

Incubation period.—The incubation period ranges from about 19½ to 21 days. At four nests at which the eggs were marked, incubation periods from laying to hatching of the final eggs were: 19 days, 20 hours ± 6 hours; 19 days, 17 hours ± 10 hours; 19 days, 22 hours ± 10 hours; 20 days, 15 hours ± 2 hours. Two other clutches were incubated at least 20 days and one 21 days; a five-egg clutch in which one egg failed to hatch required 21 days, 6 hours.

HATCHING, DISPERSAL, DEPARTURE

Eggs begin to pip three or four days before they hatch. At this time there is brief resurgence of flight singing as the adults become increasingly restless. They fly toward intruders calling *kyow* and *oo-it* and giving Wing-up threat displays on landing, the latter call being an unmistakable indication that hatching is well along.

Usually the clutch hatches within a span of 10 to 14 hours. As in other ground-nesting species there is strong selection for synchronous hatching; at two nests I found well-pipped eggs (one contained a strongly peeping chick) that had been deserted because they were slow to hatch. Egg shells are carried off by the adults, though not usually until the chick has dried, which requires several hours; in a few nests shells of the final egg were not removed. Either parent may be present at hatching and at 10 of 15 nests both were in attendance after the first egg had hatched.

The chicks are similar to those of other calidridine sandpipers (Jehl, 1968c), especially *C. melanotos*, from which they can be distinguished by their dilated bill tip. The eyes are dark brown, legs grayish with a faint green tinge; the back of the tarsus and the base of the toes are yellowish. The egg teeth (Jehl, 1968b) are lost within a few hours of hatching.

Hatching Synchrony.—At 41 nests in 1965–1967 hatching dates ranged from 28 June to 14 July, with 80 percent of the clutches hatching between 28 June and 5 July. In general, old pairs nested earlier and with greater synchrony than pairs nesting for the first time (Fig. 5). In the Dunlin, Soikkeli (1967:165) found that all birds exhibiting “mate-faithfulness started laying within 5 days of the beginning of laying by the population.” In the Stilt Sandpiper, 70 percent of old pairs hatched young within the first five days of the hatching period as compared to 60 percent of new pairs; the figures are 75 and 50 percent if the data for 1965, which include many pairs of unknown age, are excluded.

Hatching synchrony reflects tundra conditions that prevailed when the birds arrived. In 1966, the tundra was dry and conditions were suitable

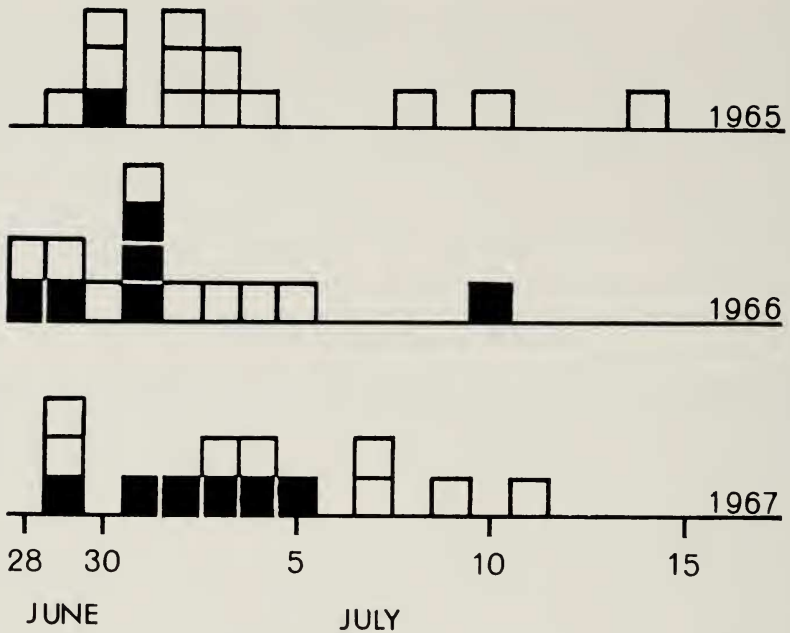


FIG. 5. Hatching synchrony of old pairs (solid squares) and new pairs (open squares) of Stilt Sandpipers, 1965-1967.

for nesting when the birds appeared. With the exception of one old pair, whose eggs hatched nine days after those of other old pairs and five days later than those of new pairs, the hatching period extended over only eight days. In the late springs of 1965 and 1967, standing water persisted in many nesting areas through early June and the hatching periods for the population extended over 16 and 14 days, respectively. I suspect that in extremely wet years, such as 1967, the emergence of insects is delayed. Consequently, some females are unable to find sufficient food for egg production and the laying period is extended. Indirect evidence of food shortage in 1967 was provided by studies of Least Sandpipers. On 10 June I found four nests each containing one egg. Three of these were deserted and at the fourth nest the second egg was not added until three days later. As the normal interval between eggs in that species is 24 hours, I infer that Least Sandpipers at least were unable to find sufficient food to produce eggs.

Dispersal.—While newly-hatched chicks are drying, the older chicks begin to wander a few feet from the nest. This causes the incubating parent obvious anxiety and hastens the eventual departure of the brood. Usually the brood

departs as soon as the last chick has dried, although broods hatched in the evening remain in the nest until the next morning and those hatched in inclement weather remain for 24 hours or more.

Departure is simple. At one nest, I watched the male arise, walk a few feet from the nest, crouch, and begin peeping softly. One by one the chicks ran to him, and within ten minutes they were being brooded 20 feet away. The female was present but made no attempt to call or brood the chicks. The entire family then disappeared into the marsh. Ten minutes later the male returned, investigated the empty nest, and flew off.

Adults are very solicitous of small chicks and leave them to direct Wing-up threat displays at approaching humans. Such challenges are invariably given from the ground and, unlike those of many other Churchill sandpipers, never from tops of small trees. Even when surprised with the brood, threat displays rather than injury feigning are the rule.

One male whose mate and nest had been destroyed a day earlier approached in response to the alarm calls of a pair of Dunlin whose chicks I was banding. He directed threat displays at me, then lowered his breast feathers, made scraping movements, and gave brooding calls. After I captured the male Dunlin, the Stilt brooded the chicks, including one I was holding in my hand.

After leaving the nest the chicks are led from the drying inland marshes to the wetter areas near the coast. The rate of movement varies with local conditions but I have found chicks two miles from the nest within two weeks of hatching. Although chicks swim well, they avoid deep water areas and occur mainly at the edges of marshes or along dry ridges, where they feed on surface-dwelling invertebrates. I have never seen small chicks attempt to probe for food, nor have I observed adults make any attempt to feed young or to direct their attention to food.

From the time they leave the nest chicks are almost always hidden from the parent's sight by vegetation and communication within the family group is almost entirely vocal. Both parents attend the brood for several days, in some cases one week, but the females soon disappear. Males remain with the chicks for about two weeks before deserting them. At that time the chicks are fully independent, although they do not develop flight capabilities until they are 17-18 days old. It is extremely unusual to encounter both parents with chicks more than one week old. In late July 1965 I found two adults defending what appeared to be a single brood of well-grown chicks: when collected, however, both proved to be males.

Prior to attaining flight the young are extremely inconspicuous. After that event they emerge from the marshes and feed openly near drying tundra ponds and soon begin to congregate in small flocks.

TABLE 1

DIFFERENTIAL MIGRATION OF ADULTS IN FALL AS INDICATED BY SPECIMENS TAKEN ON THE NESTING GROUNDS

Date	Churchill, Manitoba		All nesting grounds (including Churchill)	
	♂	♀	♂	♀
1- 5 July	4	3	7	7
6-10 July	3	3	7	5
11-15 July	8	1	9	1
16-20 July	2	1	5	1
21-25 July	4	0	8	0

Departure.—In the first days of July, small groups of migrants from farther north can be seen flying eastward along the Hudson Bay coast and transient flocks begin to appear on coastal ponds. At the same time local birds resume flocking in inland marshes. Flocking actually begins in mid-June, when small groups of males relieved from incubation congregate at feeding ponds in the early evening. Flocks gradually increase so that by late June groups of up to 15 birds may be encountered. With the start of the hatching period the flocks disappear but form again in early July, when females desert the brood. These do not persist for long and by 10 to 12 July most adult females have departed, the latest date being 17 July. Males leave the chicks by mid-July, some apparently departing the nesting grounds without joining flocks. After 18 July in most years it is extremely rare to find an adult in the inland marshes. In 1964, a late season, males departed by 21 July, and despite an intensive search over the next ten days I saw only one additional adult. In 1966 virtually all local adults left prior to 16 July, and between 16 and 22 July I found only two adults caring for late broods.

The early departure of adult females is confirmed by a small series of specimens collected at Churchill and elsewhere on the breeding grounds over the past three decades (Table 1) and by specimens from the northern United States (Jehl, unpubl.). According to McNeil (1970), both sexes are present among flocks arriving in Venezuela in early August.

Juveniles are less than a month old when they begin to disappear from the nesting grounds. The peak of migration occurs in the first week of August. Young birds from farther north pass through the Churchill area through 15 August, and stragglers occur until the end of the month.

TABLE 2

CLUTCH SIZE AND HATCHING SUCCESS OF STILT SANDPIPERS AT CHURCHILL, MANITOBA
1964-1967

Year	Clutch size					Hatching success by year (eggs hatch/ eggs laid).
	2	3	4	5	\bar{x}	
1964	—	—	2	—	4.0	8/8 (100%)
1965	2	—	11	—	3.69	41/48 (85.5)
1966	—	2	12	—	3.86	43/54 (79.6)
1967	—	2	10	2	4.0	46/56 (82.3)
Total	2	4	35	2	3.86	138/166 (83.2)
Hatching success by clutch size	4/4 (100%)	10/12 (83.4%)	117/140 (83.6%)	7/10 (70%)		

PRODUCTIVITY AND MORTALITY

Data on clutch size and hatching success are given in Table 2. There were no important annual differences in hatching success, and success was high regardless of clutch size. At neither of the five-egg clutches were all the eggs hatched successfully, which suggests that adults were unable to incubate the larger clutch effectively (cf. Maclean, 1972).

In this study inclement weather had no effect on nesting success; birds incubated through light snowfalls and up to five days of continuous rain. Heavy snowfalls, however, may lead to desertion of the nest (Farley, 1939).

The following causes of hatching failure were noted at 43 nests followed to completion; the first figures refer to number of eggs, the second, in parentheses, to number of nests involved: predation—9(3); scientific collecting—8(2), unknown—3(2); infertile—2(2); disappeared—2(2); egg cracked (due to trapping?)—2(2); desertion of pipped egg that failed to hatch on time 2(2).

Of the avian predators, Parasitic Jaegers (*Stercorarius parasiticus*) posed the greatest threat to sandpiper nests, and several eggs were known to be destroyed by these birds. Short-tailed weasels (*Mustela erminea*) and red foxes (*Vulpes fulva*) are the only important mammalian predators in the Churchill region. One incubating female was thought to have been killed by a weasel.

In three instances the death of one member of a pair led to nesting failure. One female was killed by a predator while incubating and two other females were collected by me off the territory. At each nest the eggs were pipped

but the male alone was unable to hatch them successfully, and the chicks died of exposure when he left the nest to feed. The long and almost unbroken incubation periods in this species may be advantageous in minimizing change-over and other activity near the nest, and therefore in preventing predators from locating the nest. However, this rigid system also seems to preclude adaptive adjustment by one member of the pair if its mate is killed or is unable to perform its role.

Losses of young.—Data on posthatching mortality are few because chicks are extremely difficult to find after they leave the nest. Mortality appears to be relatively high among very young chicks, and I doubt that fledging success far exceeds 50 percent. Broods of four are rarely encountered more than a few days after hatching, and after two weeks most broods consist of two, rarely three, young. As noted above, small chicks usually feed out of the parents' sight and return only for brooding. Many become lost in the high vegetation and fail to rejoin the family. This appears to be the most important cause of chick mortality. Some are "adopted," as evidenced by the not uncommon occurrence of broods with chicks of widely differing ages.

I have no direct evidence of chick loss to predators. Once I observed a pair of adults in pursuit of a Parasitic Jaeger, but it was impossible to determine whether the jaeger had made a kill.

Adverse weather conditions such as prolonged rainy periods at hatching time (see Jehl and Hussell, 1966) could lead to chick loss. The large yolk-sac enables newly hatched chicks to fast for about two days if necessary. Slightly older chicks that must leave the shelter of the adult to feed would be presumably more susceptible to inclement weather.

Food shortage is probably not a significant cause of chick mortality in most years for chicks hatching in late June or early July. Soon thereafter, the inland marshes dry out, the number of emerging insects diminishes, and chicks hatched later may find food in short supply if they are unable to reach wet areas near the coast.

I have few data on post-fledging survival. Only one of 81 chicks banded in 1964–1966 was recovered, and it was defending chicks 300 m from its banding site. I occasionally encountered banded birds whose nest could not be located; those collected invariably proved to have been banded as adults. Dunlin may breed in their first summer (Holmes, 1966a), although in Finland most do not breed until their second year (Soikkeli, 1967). The extremely low recovery rate in Stilt Sandpipers as compared to Dunlin (Soikkeli, 1967:188) indicates that Stilt Sandpipers probably do not breed in their first year. Further, the rarity of unmated birds on the nesting ground suggests that most first-year birds summer farther south.

Adult mortality.—Because site tenacity is strong in some sandpipers, one

can estimate the annual mortality rate of adults by assuming that birds not found in subsequent years have died (see Soikkeli, 1967).

Forty-one Stilt Sandpipers trapped at the nest between 1964 and 1966 were known to be alive at the end of the nesting season; 19 were recaptured one year later, 9 two years later, and one three years later. Calculated annual mortality rates ranged from 36 to 52 percent, with a mean of 47 percent, but these are much too high for several reasons: 1) Several birds not observed one year after banding returned two years later. 2) Banded birds whose nests could not be found were seen each year; these were certainly banded locally. 3) The potential for band loss is high, and although loss within one year is unlikely, loss within two years is probable (Jehl, 1969). 4) A few birds were collected in each year of this study. As shown above, a bird whose mate does not return probably does not nest in that year and soon leaves the territory. Consequently the chance of observing that bird is far less than of finding a nesting pair. All these factors tend to inflate the apparent mortality rate. Soikkeli (1967:179) found a mean adult mortality rate of 27 ± 3 percent for Dunlin in Finland; a similar rate for Stilt Sandpipers seems reasonable.

FEEDING

Stilt Sandpipers do not feed on the territory except in early spring when territorial boundaries are being established. At that time the nesting grounds may be partially covered with meltwater, so the birds forage mainly on dry ridgetops, around clumps of sedges, or at the edges of tiny depressions filled with melting snow. For most of the summer they feed in small groups in the vicinity of tundra ponds. Initially they tend to feed in marshes at the pond margins, where they peck at the ground surface for small insects. By mid-June pond life increases and the depth of the ponds decreases so that the birds are able to forage in their characteristic fashion—wading belly deep, bill and face, sometimes the entire head, immersed below the water surface. The birds walk slowly and seem to gather most if not all of their food by deliberate thrusts at organisms detected visually (see Burton, 1972). Later in summer as the ponds become shallower many birds feed on the newly-emergent mudflats along the shore, often probing the soft muck in typical calidridine fashion. The location of the feeding ponds bears no obvious relationship to the nest site. I have often seen birds a mile or two from their territories and one female was collected five miles from her nest.

Stomach contents of 39 adult birds were retained for examination. This sample, collected over four years, was too small for detailed study, and contents of many stomachs were digested beyond all but the broadest identification, e.g., adult winged insects. Nevertheless, it was evident that Stilt Sand-

pipers feed on a relatively small spectrum of food, and that they feed opportunistically, because the stomach contents of the majority of birds contained largely or entirely the remains of one prey item.

The observed feeding patterns are in accord with what might be predicted from the foraging patterns outlined above. Early in spring (29 May to 10 June) the variety of available food is limited and birds seemed to feed to a large extent on adult beetles judged by fragmentary exoskeletal remains; of nine birds collected in this period, five had also fed extensively on small seeds. The variety of food taken increased between 11 June and 30 June, largely as a result of the shift to pond habitats and the emergence of some insects. Yet, no single prey item was found in more than three of the 10 stomachs examined. The major food resources at this period, included 1) larval dystiscid beetles and small snails, and 2) seeds and adult dipterans and other flying insects; insect larvae of several families were found in a few birds but their volume was miniscule. Between 1 and 10 July adult beetles and water bugs and larval dytiscids seemed to comprise the bulk of the diet, being present in four of the eight stomachs examined; seeds were found in three birds, but none contained snails. From 11 to 26 July adult beetles, snails, seeds, and larval dytiscids, in decreasing order of abundance, were the commonest prey items of 12 birds; but, as in samples taken earlier in the summer, no single item predominated and other larval insects were virtually absent.

Data on nine birds from 6 days to three weeks in age are too few for analysis. It appears that for about 10 days chicks feed entirely on surface-dwelling forms including adult winged insects; larval dytiscids were not found in birds less than an estimated 12 days old but were common in three of five older chicks; two of four flying juveniles, about three weeks old, had fed extensively on larval chironomids.

Holmes (1966c) found that Dunlin at Barrow fed largely on insects, particularly on dipteran larvae, Tipulidae in June and August, Chironomidae in midsummer. Further, Holmes and Pitelka (1968) demonstrated wide overlap in foods taken by four sympatric calidridine sandpipers at Barrow. I found tipulid larvae in only one Stilt Sandpiper stomach, where they constituted the entire contents, and chironomid larvae in only six; and, with the exception of dytiscids, larval insects constituted only a small fraction of the Stilt Sandpiper's diet. This suggests, as one would predict on morphological and behavioral evidence, that the Stilt Sandpiper is able to avoid food overlap with other calidridines by exploiting pond habitats. The possibility of interaction with other species utilizing pond habitats at Churchill (Short-billed Dowitcher, Hudsonian Godwit, Northern Phalarope) remains to be determined.

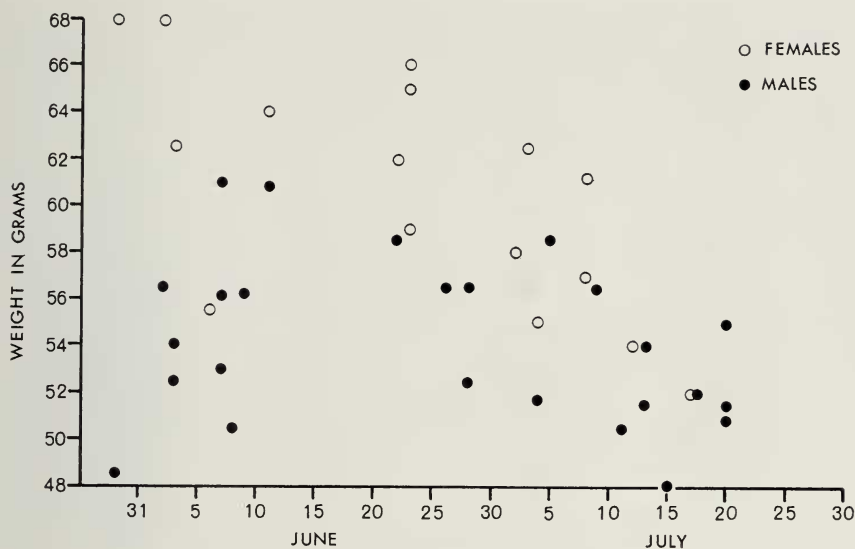


FIG. 6. Seasonal weight changes in Stilt Sandpipers.

WEIGHTS

Weights of nine chicks, all less than 24 hours old, averaged 8.1 g (range 7.3–9.9). Two barely flying chicks, estimated age 17 days, weighed 43 and 48 g.

The mean weight of 24 males collected at Churchill was 53.8 g (range 48.0–60.8), that of 15 females 60.9 g (range 52.0–68.0). Seasonal variation in weights of adults are plotted in Figure 6. Birds collected soon after arrival in late May and early June possess little or no subcutaneous fat deposits. Females are heaviest immediately upon arrival and show a gradual weight loss through the summer. Males seem to be lightest while they are establishing territories and defending chicks. As neither sex shows any evidence of weight increase prior to migration it may be inferred that the first migratory flights are short, perhaps extending no farther than to the northern United States. Migrants in southern Canada and the northern United States average heavier: two adult males from Michigan each weighed 60 g; Woodford (1958) removed 19.2 g of fat from a 75 g male collected in Ontario in early August; two adult females from Michigan and New Jersey weighed 60 and 67.5 g, respectively; seven juveniles from Michigan and Minnesota averaged 61.0 g (range 47.4–78.6). According to McNeil (1970) the heaviest birds have sufficient fat reserves for non-stop flights from southern Canada to northern South America.

MOLT

The first prebasic molt of Stilt Sandpipers, like that of the Dunlin (Holmes, 1966*b*) is largely confined to the body tracts. It begins in August, before the young leave the nesting grounds, and seems to be largely completed by mid-September in most individuals. However, McNeil (1970) reported that young birds arriving in Venezuela in November were just finishing molt. Succeeding, prebasic molts are more extensive, and involve the entire plumage. Molt begins on the neck and chest and spreads anteriorly and posteriorly. Adults may begin molting as early as 2 July, while still incubating, but most birds do not start until about 10 July. Extensive molt is evident in all body tracts by mid-July, but the flight feathers are not replaced until after adults leave the nesting grounds. Four adults collected in southern California on 2 September 1963 had replaced all but the outermost primary and molt of the rectrices was well advanced. McNeil (1970) suggested that molt may be suspended during migration as adults arriving in Venezuela in early August showed no active molt. Molt was resumed upon arrival and was largely completed by the end of September.

The prealternate molt begins in January and ceases by late March or April (McNeil, 1970: Fig. 23). The extent of this molt is variable and may change from year to year in the same individual. All birds replace the body plumage and about 90 percent molt the tertials; one bird that molted tertials in 1966 did not in 1967. The remiges are not molted; approximately 60 percent of the birds also retain all wing coverts, the remainder molt only one or two of the proximal median and lesser secondary coverts. One bird molted the entire series of median secondary coverts, four proximal, and a few lesser secondary coverts. The limited data indicate no relationship between the extent of molt and age.

The prealternate molt of the rectrices is also variable, the most common patterns being the loss of the central pair (or two pairs) of rectrices, and loss of all but the central pair; a few birds replace the entire tail, some only one or two feathers, and a few apparently do not show molt. As with the wing coverts, the extent of tail molt varies from year to year and only three of eight birds trapped in two consecutive years showed identical molt patterns.

Stilt Sandpiper rectrices are usually gray-brown distally, fading to whitish at the base. The coloration of rectrices renewed in the prebasic molt is fairly uniform, but the color patterns of those renewed in the prealternate molt is variable (Fig. 7). To determine the significance of this variation, I scored the variant patterns in four categories ranging from plain and unmarked ("1") to strongly barred ("4"). In addition, I plucked and retained the central rectrices of many birds for future comparison. In 11 of 15 birds

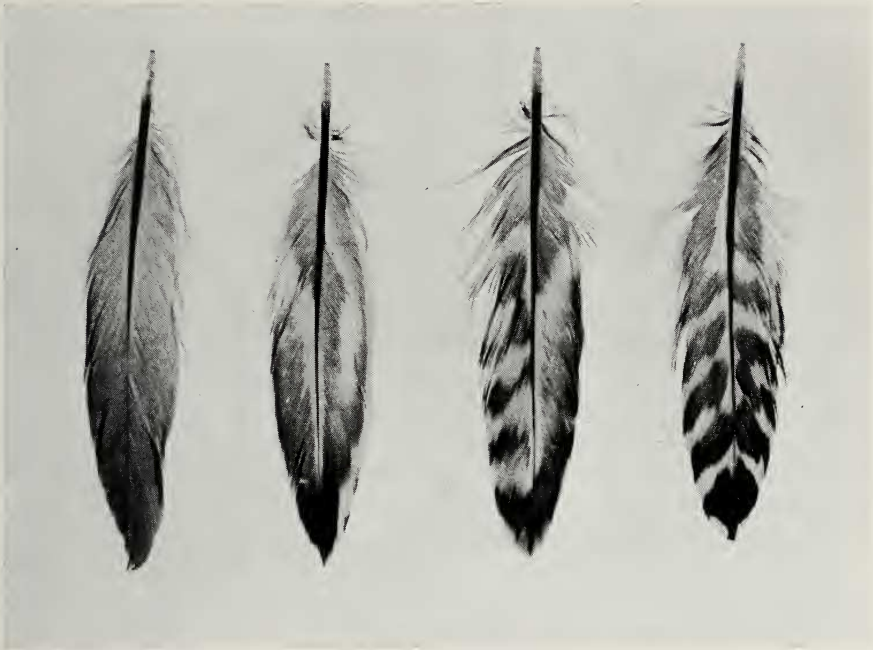


FIG. 7. Variations in rectrix pattern of adult Stilt Sandpipers. From left to right, the feathers illustrate categories "1" through "4" (see text for explanation).

caught in two or more years, the pattern of central rectrices was unchanged or changed no more than one category; female 66-F, for example, ranked "1" in 1965, "2" in 1966, and "2-3" in 1967. Two birds changed from "4" to "1" and two from "1" to "4"; for example, male 65-F ranked "1" in 1965 and 1966 but "4" in 1967; male 65-M, "4" in 1965, "1" in 1966, and "2" in 1967. The annual variations, therefore, are usually slight, may occur in either direction, and do not indicate either age or sex.

SYSTEMATICS

Geographic variation.—In this study I examined 427 specimens of Stilt Sandpipers of which 231 (115 adults, 48 juveniles, 70 downy young) were collected on the breeding grounds (Fig. 1). The sample was geographically biased, with 71 of the adult specimens coming from the vicinity of Churchill, Manitoba. Nevertheless, I found no evidence of geographic variation in either size or coloration.

Relationships.—It is well established that the Stilt Sandpiper is a member of the Calidridinae (Lowe, 1915; Peters, 1934; Jehl, 1968c), and one suspects

that if *Micropalama* bred in Europe, Witherby et al. (1940:227) would have included it in their expanded genus *Calidris*. They defined that genus to include a number of small to medium-sized sandpipers with variable bill morphology but in which the bill averaged longer than the tarsus. This definition would seem to exclude the long-legged *Micropalama*; yet, its bill/tarsus proportions are surprisingly similar to those of more typical species. For example, bill length exceeded tarsus length on 10 of 71 Stilt Sandpipers trapped and measured at Churchill, as well as in only 12 of 80 Least Sandpipers. Thus, the generic distinctness of *Micropalama* on morphological grounds is tenuous at best, and behavioral evidence indicates no significant differences between *Micropalama* and some unquestioned members of *Calidris*. In view of the broad genera that are currently recognized by most shorebird taxonomists there are no compelling reasons for considering *Micropalama* as distinct. The important question, however, is not whether this monotypic genus should be retained, but, rather, to which of the calidridine sandpipers is the Stilt Sandpiper most closely related.

There are no reasons for inferring a close relationship between the Stilt Sandpiper and the small calidridines or "peep," or to other monotypic calidridines (*Philomachus pugnax*, *Tryngites subruficollis*, *Limicola falcinellus*, *Aphriza virgata*, *Eurynorhynchus pygmeus*). On the other hand, aspects of morphology, territoriality, breeding behavior, and vocalizations suggest its affinity to such species as the Knot (*C. canutus*), Dunlin, and Curlew Sandpiper (*C. ferruginea*).

Of the species for which adequate comparative data are available, the Stilt Sandpiper seems to be most closely allied to the Curlew Sandpiper. The general morphological resemblance in body size and proportions between the two species is striking (cf. Holmes and Pitelka, 1964: Fig. 2, and Parmelee et al., 1967: Plate 5); both species have relatively long, decurved bills; and females average slightly larger than males. The juvenal and winter plumages of the two species are similar and the distinctive breeding plumages also share certain similarities; in both the abdomen is patterned and males are more highly colored than females. Transversely barred underparts characterize the Stilt's breeding plumage, but male Curlew Sandpipers are also similarly barred with black on the chest. Rump and tail patterns of these species are virtually identical, and the peculiar barred rectrices described above are also found in approximately 30 percent of adult Curlew Sandpipers. (I found similarly-patterned feathers in nine of 181 adult Dunlins, but in no other calidridine).

Both Curlew and Stilt Sandpipers have unusually varied and complex vocalizations. Holmes and Pitelka (1964) described those of the Curlew Sandpiper in detail and noted (p. 368) that the "basic resemblances in



FIG. 8. The approximate breeding ranges of the Stilt Sandpiper (black) and the Curlew Sandpiper (cross hatched). Data, in part, from Holmes and Pitelka, 1964, and Portenko, 1959.

phrasing and other features are striking" between the two species. They commented particularly on the similarity in flight songs (cf. Holmes and Pitelka, 1964, Fig. 4 with Fig. 3 herein), and noted that both species followed the flight song with a series of "whine notes."

Behavior.—General patterns of aerial courtship in the two also seem similar, except that the display flight of the male Stilt Sandpiper is given with wings upraised, of the Curlew Sandpiper with wings held horizontally. In both territorial displays are particularly wide-ranging; in the Curlew they are performed at low elevations, in the Stilt fairly high. Both use the whine note in territorial defense, the Curlew Sandpiper mainly from the ground, the Stilt Sandpiper from the air. Both have a ground announcement display to indicate that the territory is occupied; in the Curlew Sandpiper the whine note is used in this display, in the Stilt Sandpiper the *errit* call.

Holmes and Pitelka (1964) stated that the whine note was "absent in the other eight species of *Calidris*" they had studied, and they also noted the absence of ground announcement displays in those species. Parmelee et al. (1967) commented on the similar territorial and courtship behavior of Knots and Stilt Sandpipers. Descriptions of the Knot's territorial call (Parmelee and MacDonald, 1960; Hobson, 1972) are reminiscent of the Stilt's whine-note, which suggests that the Knot is more closely allied to this species than is currently acknowledged.

Ground displays of the Curlew Sandpiper are apparently much more conspicuous and complex than those of the Stilt Sandpiper, but the most pronounced difference is the role of the sexes in nesting. In the Stilt Sandpiper the pair bond persists through the nesting season, both sexes incubate, and the male remains longest with the brood; in the Curlew Sandpiper the pair bond is transitory and only the female incubates (Holmes and Pitelka, 1964; Portenko, 1959) and cares for the young. The ecological advantage of a short pair bond in high arctic sandpipers has been argued by Pitelka (1959; see also Holmes and Pitelka, 1968). Its taxonomic implications, if any, remain to be determined.

Biogeography.—The occurrence of many closely related shorebird taxa on opposite sides of the Bering Straits is evidence of the importance of this barrier in shorebird evolution. The occurrence in Alaska of an ice-free region, the Bering Sea-Yukon refugium, in the Pleistocene also provided opportunity for the isolation and subsequent divergence of some populations (e.g., Rand, 1948; Pitelka, 1950; Cade, 1955; Fay and Cade, 1959), one result being the evolution of a distinctive Alaskan shorebird assemblage.

In Table 3 I have outlined the general distributions of some shorebirds occupying the Bering Straits region and their close allies. This table does not include all possible species pairs in that area (see Larson, 1957) and some of the relationships suggested are admittedly unconfirmed; for example, *Calidris ptilocnemis* may be more closely related to *C. alpina* than to *C. maritima*; Pitelka (1959) questioned whether *C. melanotos* was particularly close to *C. acuminata*; and Holmes (pers. comm.) has suggested that *C. mauri* is more closely allied to *C. fuscicollis* than to *C. pusilla*. Despite these uncertainties, the isolating influence of the straits and the refugium is unquestionable. The allopatric distribution of the Curlew Sandpiper and Stilt Sandpiper (Fig. 8), in addition to their morphological and behavioral similarities, suggests that these species also have diverged from a common ancestor in this region.

In a speculative attempt to reconstruct evolution in the Charadrii, Larson (1957) outlined climatic and geographic conditions during the Tertiary and

TABLE 3

BIOGEOGRAPHIC RELATIONSHIPS OF CLOSELY RELATED SHOREBIRD TAXA IN THE
BERING STRAITS REGION

North America	Bering Sea- Yukon refugium	Asia	Refer- ence ¹
<i>Charadrius semipalmatus</i>	————	<i>C. hiaticula</i>	h
<i>Pluvialis d. dominica</i>	————	<i>P. d. fulva</i>	h
<i>Limosa haemastica</i>	————	<i>L. limosa</i>	d
————	<i>Limosa lapponica baueri</i>	<i>L. l. menzbieri</i>	e
<i>Numenius p. phaeopus</i>	<i>N. tahitiensis</i>	<i>N. p. variegatus</i>	d
<i>Numenius borealis</i>	————	<i>N. minutus</i>	d
<i>Tringa solitaria</i>	————	<i>T. ocropus</i>	d
<i>Heteroscelus incanus</i>	————	<i>H. brevipes</i>	d
<i>Actitis macularia</i>	————	<i>A. hypoleucos</i>	d
<i>Arenaria interpres</i>	<i>A. melanocephala</i>	<i>A. interpres</i>	d
<i>Limnodromus griseus</i>	<i>L. scolopaceus</i>	<i>L. semipalmatus</i>	g
————	<i>Aphriza virgata</i>	<i>Calidris tenuirostris</i>	b
<i>Calidris pusilla</i>	<i>C. mauri</i>	<i>Eurynorhynchus pygmeus</i>	a
<i>Calidris minutilla</i>	————	<i>C. subminuta</i>	c
<i>Calidris melanotos</i>	————	<i>C. acuminata</i>	f
<i>Calidris maritima</i>	<i>C. ptilocnemis</i>	————	c
<i>Micropalama himantopus</i>	————	<i>C. ferruginea</i>	i
<i>Tryngites subrujicollis</i>	————	<i>Philomachus pugnax</i>	c

¹ Reference: a, Burton, 1971. b, Jehl, 1968d. c, Larson, 1957. d, Mayr and Short, 1970. e, Portenko, 1936. f, Portenko, 1968. g, Rand, 1950. h, Vaurie, 1964. i, this paper.

Pleistocene that led to the isolation and subsequent divergence of previously widespread populations. These included major oceanic barriers and shifting glacial refugia during the Pleistocene. According to Larson, members of the evolving species pairs tended to occupy climatic regions similar to those utilized by the ancestral populations. One of his conclusions (1957:59) was that during interglacial periods the Eurasian component of a stenothermal cold species pair was probably destroyed more often than was its North American counterpart, which accounted for the existence of so many monotypic North American genera (*Aphriza*, *Micropalama*, *Tryngites*). However, it appears that for *Micropalama* and *Aphriza* (Jehl, 1968d) close relatives are alive and well on the Asian side of the Bering Straits, and the European member of the species pair with *Tryngites* is certainly *Philomachus*, as Larson (p. 50) admits. Thus, the suggested differential extinction of Eurasian

representatives of presumed species pairs seems doubtful. In fact, only one monotypic genus of the Calidridinae, *Limicola*, has no obvious close allies (Burton, 1971), and it is absent from North America, not Eurasia.

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SUMMARY

A banded population of Stilt Sandpipers was studied at Churchill, Manitoba, in the summers of 1964-1967. The species arrives in late May or the first days of June, with males tending to arrive a day or two in advance of females. Mate and territorial fidelity is high. Experienced breeders return to their nesting territories in well-drained sedge meadows, where they encounter their mate of the previous year. Nesting begins almost at once; often the old nest scrape is re-used. There is no evidence that birds form pair bonds during migration. The apparent en route pairing that has been alleged in several species of arctic sandpipers can be attributed to the strong homing ability and site fidelity of experienced breeders.

The complex vocalization of the Stilt Sandpiper, and the contexts in which they are used, are outlined. Territories are established and maintained through aerial displays. Territorial defense wanes about a week after the clutch is completed, at which time late-nesting pairs may be able to nest in close proximity to established pairs. Nesting behavior is described in detail. The role of the sexes in incubation is rigid, with males incubating by "day" (05:00-19:00), females by "night." Males are capable of breeding immediately upon arrival, but females do not attain breeding condition until several days later. Gonadal regression occurs about a week after the clutch is completed and after that time re-nesting seems impossible. The incubation period averages about 20 days. In most years the peak of hatching occurs in the first days of July, old pairs hatching young, on the average, a few days earlier than pairs nesting for the first time. The chicks are led from the drying sedge meadows to wet areas near the coast. Females remain with the brood for about a week, males for two weeks, before migrating. Most chicks leave the Churchill area by mid-August. In this study predation was the major cause of nesting failure. Separation from the adults and adverse weather are probably the major sources of chick mortality.

Stilt Sandpipers do not feed to any appreciable extent on the territory, but forage in small tundra ponds up to five miles from their nests. Analysis of stomach contents suggests that by exploiting pond habitats the species is able to avoid food overlap with most other sandpipers.

Body molt of adults begins in July, after the chicks have hatched, but flight feathers are not molted until after the birds migrate from the nesting areas. Variations in the molt pattern do not seem to be associated with age or sex.

No geographic variation was detected in this species. There are no strong reasons for maintaining *Micropalama* as a monotypic genus distinct from *Calidris*. Evidence from behavior, morphology, vocalizations, and biogeography indicates that the Curlew Sandpiper (*C. ferruginea*) is the closest relative of the Stilt Sandpiper.

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